

A New Species of the Devonian Lungfish *Dipnorhynchus* from Wee Jasper, New South Wales

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ABSTRACT. A new large mandible of *Dipnorhynchus* from the Early Devonian *serotinus* Zone (late Emsian) at Wee Jasper, is given the status of a new species, *D. cathlesae* n.sp. This fossil characterised by its size; relative depth with respect to its length; short anterior furrow, deeply bordered by a raised broad rim of dentary between itself and the labial pit; large foramen for a nerve in the posteromedial end of the labial furrow; a strong furrow from the adductor pit to the posterior end of the labial pit; thick dentary; lack of tubercles (blisters) on the prearticular plate; and an adductor pit wide posteriorly and narrowing gradually anteriorly. The surface of the tooth plate is not made of dentine, but of bone formed on the surface of the prearticular. This species represents the youngest known occurrence of *Dipnorhynchus* in the Murrumbidgee sequence.

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Early Devonian dipnoans were beginning a period of rapid evolution. The number of species is limited at present, but many of them are beautifully preserved in limestone, and can be extracted as three dimensional fossils with acetic acid. The specimens from Wee Jasper on the Burrinjuck Dam, New South Wales, are among those that have produced the best information on undistorted material. *Dipnorhynchus* is the most abundant of these genera. Herein we describe a new species of *Dipnorhynchus*, *D. cathlesae*.

The limestone-shale sequence at Wee Jasper and Taemas covers a range from the *dehiscens* Zone to the *serotinus* Zone of the Emsian. The rocks are more or less continuously fossiliferous and include many marine invertebrate fossils including corals and brachiopods. Remains of the dipnoan

Dipnorhynchus have been previously described from several levels at both Taemas and Wee Jasper, but a recent discovery of a mandible of this genus towards the top of the sequence provides information on its subsequent evolution. The specimen was discovered by Ian and Helen Cathles of Cookmundoon Station, Wee Jasper.

Most of the rocks were deposited in shallow subtidal environments, but occasional supratidal deposits are also found. All the specimens of *Dipnorhynchus* were found in the subtidal limestones.

The specimen herein described shows large neural openings into a labial pit, the outer edge is formed by a high margin of the surangular; reduced dental structure (tubercles) on the prearticular; and the great height of the

Table 1. Comparison between the dimensions of the holotype of *Dipnorhynchus cathlesae* and the largest known specimen of *Dipnorhynchus kurikae* Campbell & Barwick (ANU 60030).

species	width at mandibular articulation (cm)	length (cm)	maximum depth of mandible (cm)	maximum depth of dentary (cm)
<i>D. cathlesae</i>	22	19	10	6.5
<i>D. kurikae</i>	15	14	5.5	3

posterior face of the mandible leaving a shallow space for the tongue mass. We interpret these features to mean that the suction capacity of the animal was increased beyond what is shown by the earlier species, that the tooth plates were modified to be crushers of food, and that the capacity of the hyoid apparatus to move forward and backwards was greatly reduced.

This specimen is so large that when it was first observed in the rock, it was not recognised as a dipnoan. The major dimensions are outlined above (Table 1), and are set against the largest known specimen of *D. kurikae* (Campbell &

Barwick, 1985). Note that *D. kurikae* is dwarfed by the specimen of *D. cathlesae*, especially in its depth.

The specimen was exposed on the rock surface and its posterior face was weathered. It was collected in five fragments, four of which were in association and one was isolated. The associated fragments were separated by cracks and breaks in the rock, and they fell apart on collection. Reassembly showed that fragments of bone were missing from some of the edges, but by and large the fragments could be restored sufficiently to permit us to make a description of most of the osteological features. The isolated

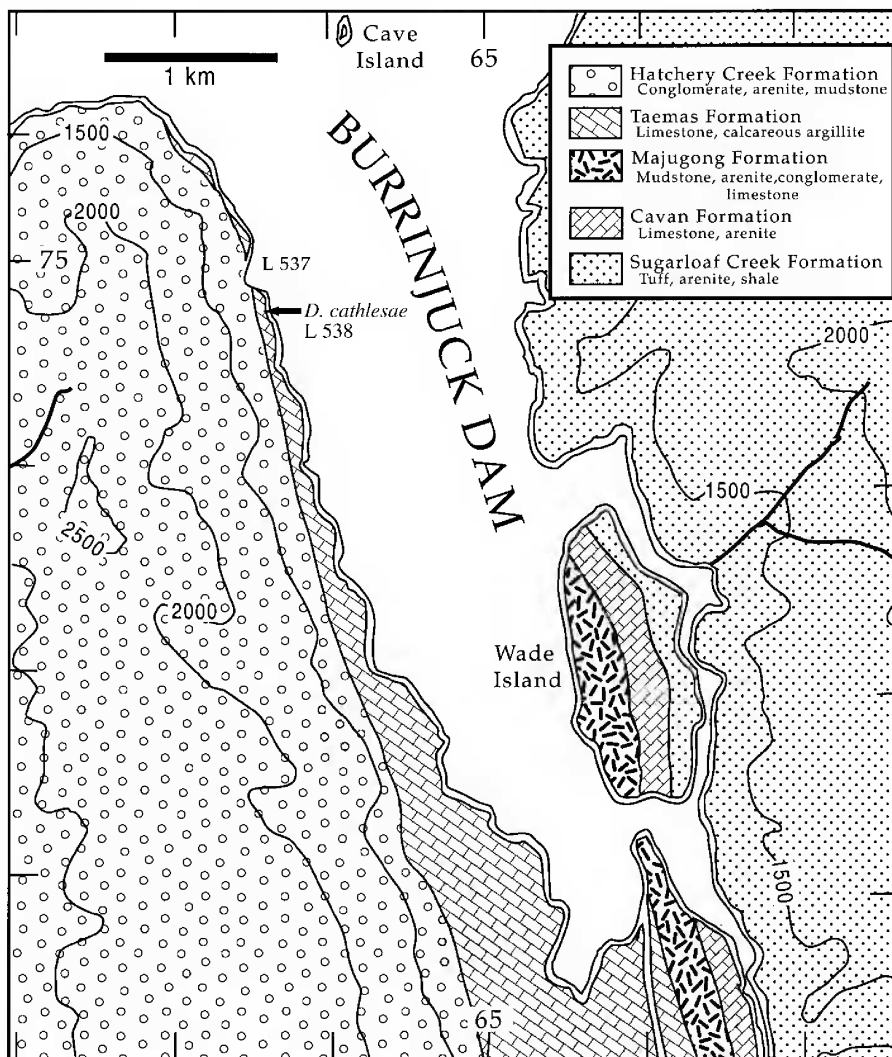


Figure 1. Map of the northern part of the Wee Jasper outcrop of the Lower Devonian Limestones, modified after Pedder *et al.* (1970). The numbers L 537 and L 538 refer to the collection data of Pedder *et al.*

Top of the Taemas Formation, Wee Jasper

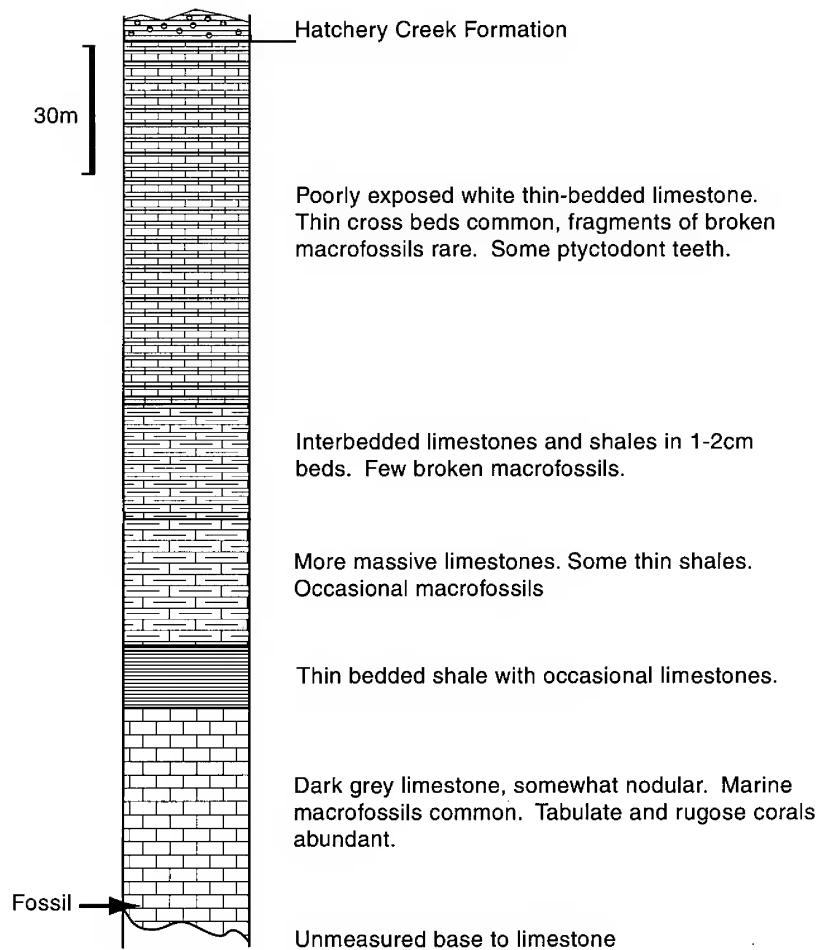


Figure 2. Stratigraphic section measured from the locality where *Dipnorhynchus cathlesae* was collected up to the Hatchery Creek Formation.

fragment was found down slope from the original specimen, and consists of a piece of a mandible that fits a section missing from the original. No other bone fragments are found in the vicinity and the bone size in the fragment matches the main specimen.

In the absence of other bones in the sediments around the point where the specimen was recovered, and despite several detailed searches in the surroundings, which are well exposed because the withdrawal of the waters of the Burrinjuck Dam in the 1998 drought, we conclude that any other specimens of the species that lived in the area have not been preserved in observable rocks. In the sediments overlying the specimen there are several layers of limestone containing ptyctodont fragments, but these rocks have not yielded any large fragments of bone.

Stratigraphy

A map showing where the specimen was collected is given in Fig. 1, and the stratigraphic sequence of the upper part of the Taemas limestone at Wee Jasper is presented in Fig. 2.

The uppermost unit below the Hatchery Creek Formation consists of very thin bedded white limestones, many beds being only 1 mm thick. The unit is c. 69 m thick. Some crossbedding is present. The rocks are interpreted as an intertidal zone carbonate deposit, which is consistent with the fact that the overlying unit is the fresh water Hatchery Creek Formation. The limestone has few invertebrate macrofossils, but ptyctodont tooth plates are occasionally present.

Immediately beneath this unit are three strata consisting of interbedded limestones and shales. These contain few macrofossils, but occasionally they have a few ptyctodonts. Together these three units are c. 58 m thick.

Our specimen comes from c. 40 m below the top of the limestone beneath the above mentioned three units, near the locality listed as by Pedder *et al.* (1970) as L538 at the northern end of the Taemas limestone outcrop. This lower limestone is different in kind from those lying above it, being a dark grey colour, often nodular, and in units some centimetres thick. It was deposited in an environment which supported a rich marine life. The commonest fossils are the thamnoporoid and favositid tabulates associated with an

abundant ceroid syringoporoid probably related to *Romeripora* (Hill & Jell, 1970). The corals are all rolled and show a variety of shapes, indicating that at least during the final depositional event, a rough water environment existed. The rugosans have been described by Pedder in Pedder *et al.* (1970), and fig. 4 of that paper lists seven species of corals which are restricted to this level. Garratt & Wright (1989) have indicated that this unit belongs to their Coral Zone F. The conodonts were also described by Philip & Jackson in Pedder *et al.* (1970), and subsequent work outlined by Basden *et al.* (1999) indicates that they belong to the *serotinus* Zone of late Emsian age. Other fossils in the dipnoan bearing limestone include stromatoporoids and gastropods. Brachiopods are rare. The fossil site is c. 142 m beneath the Hatchery Creek Formation.

One peculiarity of the occurrence is the fact that no other bone was found anywhere in the vicinity. In the Wee Jasper sequence, fragments of placoderms are commonly found near dipnoans, but prolonged searches at this locality failed to find bone of any kind.

The locality is on the flank of the syncline of which the axis lies nearby. Hence the rocks have been subject to the cleavage which is common in the area, and the dipnoan specimen is somewhat distorted. Despite this the specimen restoration is not badly deformed.

Systematic palaeontology

Genus *Dipnorhynchus* Jaekel, 1927

Type species. *Ganorhynchus sussmilchi* Etheridge Jr., from the *Spinella yassensis* Limestone at Taemas, Burrinjuck Dam, New South Wales.

Remarks. Although we have no skull of the new species described herein, we confidently assign the mandible to *Dipnorhynchus*. It displays the main features of the mandible of that genus, and it has no evidence of teeth on the prearticulars which should be there if it were related to *Speonesydrion*, the only other genus of dipnoans found in this stratigraphic sequence.

The specimen was prepared by etching with acetic acid, so that much of the internal structure which is not visible on other more complete dipnorhynchids, was directly observable on this specimen. To hold some of the more fragile parts in position, thin wooden struts were placed in position, and these can be seen on Fig. 3.

Dipnorhynchus cathlesae n.sp.

Holotype. ANU60027, from the upper part of the Taemas limestone, near L538 on the map of Pedder *et al.* (1970). Specimen on loan from I. & H. Cathles, Cookmundoon Station, Wee Jasper.

Diagnosis. Large species with its height relative to length greater than in any other members of the genus; dentary with a high lateral edge; labial pit deep and bordered by a high margin composed of the surangular; large neural connection from the adductor cavity to the labial pit; a large groove extends

from the adductor pit to the labial pit; lingual space very shallow; no tubercles (blisters) on the prearticular tooth plate.

Remarks. Our first reaction was that the specimen was a large adult of *D. kurikae*, a species found in the *Receptaculites* and at the top of the Bloomfield Limestone, lower down in the stratigraphic sequence. The largest specimen of that species we have collected is a palate described by Campbell & Barwick (1985: fig. 5), but it is smaller than the present specimen. A number of characters found in this new specimen are of the same kind as those found in other dipnorhynchid species, but their proportions differ. On the other hand, some features are different in kind from what are known elsewhere. For these reasons we have decided to describe the specimen as a new species. We now refer to the individual characters separately.

1. In comparison with other dipnorhynchids, the **labial pit** (Figs. 5, 6B–D, 10) is a short deep structure. Its lateral edge, formed from the surangular, is high and makes a distinct margin, turned inwards along its dorsal edge and slightly overhangs the pit. Posteriorly, this edge rises up to join the edge of the surangular forming the outer edge of the adductor fossa, leaving a groove (a labial groove, Figs. 4A, 10) along the inner face of that bone. This labial groove, which is up to 6 mm in diameter, runs from the anterior margin of the adductor fossa into the lowermost margin of the labial pit. It can be traced along the inner face of the dermal bones for about 2 cm posterior to the anterior end of the adductor fossa, gradually becoming less clear posteriorly. The inturned edge of the dermal bone which overhangs it is covered by fine granules as are common along the more posterior edge of the surangular. The breadth of this granulated area is narrower than is found in specimens of *D. kurikae*.

In its depth and continuity into the adductor chamber this groove is unlike any structure which we have observed in other dipnorhynchids. In *D. kurikae*, the labial pit is shallow and does not have an upturned lateral margin. In *D. sussmilchi* the labial pit is even shallower, and its lateral margins are downturned rather than forming a rim. In *D. kurikae* a slight groove is present running along the floor of the labial pit and, running along the flattened surface of the bone behind the labial pit, it enters the adductor fossa at its *anteromedial* end. This is the boundary between the surangular and the bone forming the remainder of the floor of the labial pit. Clearly this cannot make any impression on the inner face of the surangular, and it is not in the same position as the groove in *D. cathlesae*.

Did this groove in *D. cathlesae* house a vessel, or a nerve, or a muscle or a ligament? We do not accept that it was a nerve because of its size, and because the abundant supply of nerves observed elsewhere in the labial pit make the same pattern we have observed in other dipnorhynchids (Thomson & Campbell, 1971: figs. 20, 41, 80; Campbell & Barwick, 1985: figs. 8a, 9a). In particular a large foramen at the *posteromedial* end of the labial pit passes outward from the adductor chamber through bone beneath the posterior end of the dentary. This carried a nerve from the adductor chamber to the labial pit; it also carried a branch which turns forward into the posterior end of the anterior

fossa. Because it carries the two branches, the foramen at the posterior end of the labial pit is obviously double internally but apparently single externally. The foramen joins the labial pit and the longitudinal groove by a deep furrow on the right side of the specimen, but on the left the furrow is much shallower, and has a small anteriorly directed furrow opening out of its margin. In extant dipnoans, only nerves V and VII extend forwards to this position. These would have supplied the sensory nerves to the soft tissues in the anterior furrow and the labial pit. Other nerves which enter the labial pit pass into the base of the pit via a large number of foramina (Figs. 6C,D). These open down into the adductor cavity, and they would have carried nerves and vessels which entered the labial pit. Thus we can account for a nerve and blood supply to the lip, and so there is no need for a large nerve or the provision of a blood supply from the adductor chamber through the foramen under discussion.

Therefore this labial groove must have carried a muscle or a ligament from the adductor pit to the lip. The lips of extant lungfish take an active part in the feeding mechanism (Bemis, 1987, for summary). In his comments on the lips and tongue, Bemis noted that chondroid tissue plays an important part in outlining the shape of the lips. In *Lepidosiren*, the upper and lower lips engage each other to make a surface against which the inflow of water can be controlled. *Protopterus* has a different and more complicated system. We have no reason to think that our new primitive form followed either of these patterns, but the presence of large lip spaces suggests that the ability to be a suction feeder was already present in the Devonian. Other dipnorhynchids did not have a large groove running into the labial pit as does *D. cathlesae*, and yet they probably possessed a suction feeding capacity. Hence we conclude that the capacity to produce suction feeding was present without the structure in the groove in question. However, the fact that the lips are known to be of major importance for suction in extant dipnoans, and different means for improving suction were evolved by different extant genera, it seems reasonable to infer that *D. cathlesae* had developed an improved method for suction in comparison with previous members of the genus.

As the groove runs posteriorly into the adductor fossa where it loses contact with the dermal bone and would have been adjacent to the adductor muscles, the soft tissue could have contained an offshoot from the adductor musculature. This is of interest because the lip retractor muscles of *Lepidosiren* and *Protopterus* are derived embryologically from the adductor mass (Bemis, 1987: 262). On the other hand, the groove could have contained chondroid tissue connected into the adductor muscle chamber. The information we have at present does not allow us to choose between these two hypotheses.

2. In all dipnorhynchids, the well-defined **anterior furrow** (Figs. 4A, 7A,B) is completely surrounded by bone in dorsal view. It is bounded anteriorly and laterally by the dentary, and posteriorly by the prearticular. In all the other known species of dipnorhynchids, the anterior furrow is long and narrow. In some specimens it is divided by the prearticular joining the dentary medially, but the distribution

of this feature among populations shows that it is subject to intraspecific variation. In *D. cathlesae* the anterior furrow is present and is enclosed in the usual way for a dipnorhynchid, but it is shorter and wider in dorsal view than in other dipnorhynchids. Part of this may be due to the fact that the prearticular extends slightly over its posterior end. Despite this, the furrow is less than two-thirds the length of the dentary.

The anterior end of the furrow is overhung by the dentary which turns down into the furrow, and is bounded by a strong ridge parallel with the anterior edge of the furrow. Medially on this edge there is a narrow thin protrusive layer which has the appearance of dentine. Deeper into the furrow, the dentary forms a groove which is bounded ventrally by a thin line where it joins the endoskeletal bone. On the posterior face of the anterior furrow the dental plate overhangs, leaving a groove. This groove is at about the same level as the groove in the dentary around anterior furrow mentioned above. We conclude that a layer of soft tissue formed within the anterior furrow, protecting the soft (sensory) tissue filling the lower part of the anterior furrow. Presumably this covering layer must have contained many perforations to permit interaction with the sensory tissue beneath. From its position we think that it was a chemosensory structure at the entrance to the mouth.

The floor of the furrow is formed of open textured endoskeletal bone which contains several foramina. These foramina (Figs. 7A,B) are present on both sides of the specimen, though they are differently disposed with respect to the mid-line. This is normal for dipnorhynchids (Campbell & Barwick, 1985). The right side of the specimen has at least six large foramina similarly opening downwards into either the anterior end of the adductor chamber, or the space occupied by tubules between the adductor chambers.

The posterolateral corners of the anterior furrow are strongly overhung by the edge of the prearticular dental plate. High up in the posterolateral corner of the anterior furrow is a foramen which opens via a long tube, which is entirely concealed in bone, into one of the foramina making up the large unit at the posterior end of the labial pit (Fig. 10). The second foramina in this unit also sends a nerve into the posterior end of the labial pit. This nerve would have been either V or VII, as comparison with *Speonesydrion iani* shows (Campbell & Barwick, 1984: fig. 25).

3. The **dentary** (Figs. 4A, 6B–D, 10) is much thicker dorsoventrally than that of any other dipnorhynchid. Ventrally it is not separated from the infradentaries by the slight groove which is common on all other dipnorhynchids, but it grades smoothly into the infradentaries. Along its dorsal surface the median part is smooth, depressed beneath the levels of the lateral parts, and does not support a transverse ridge. Laterally the dentary is also well rounded on its dorsal surface, and the surface continues forward to the level of the anterior end of the anterior furrow. In other dipnorhynchids the lateral surface of the dentary decreases height more posteriorly. In *D. kurikae* at all stages of growth, the dentary has a secondarily thickened ridge along the lateral crest. No sign of such a ridge is present in *D. cathlesae*. Nor is there present a thickened ridge along the anterior margins of the dentary making a distinct feature in *D. kurikae*.



Figure 3. A, ventral and B, dorsal views of the holotype of *Dipnorhynchus cathlesae*. Photographs are greatly reduced in size. Arrow indicates where sections shown on Figs. 11–14 were cut. Isolated left fragment not included in figure, see Fig. 4. Scales = 1 cm.

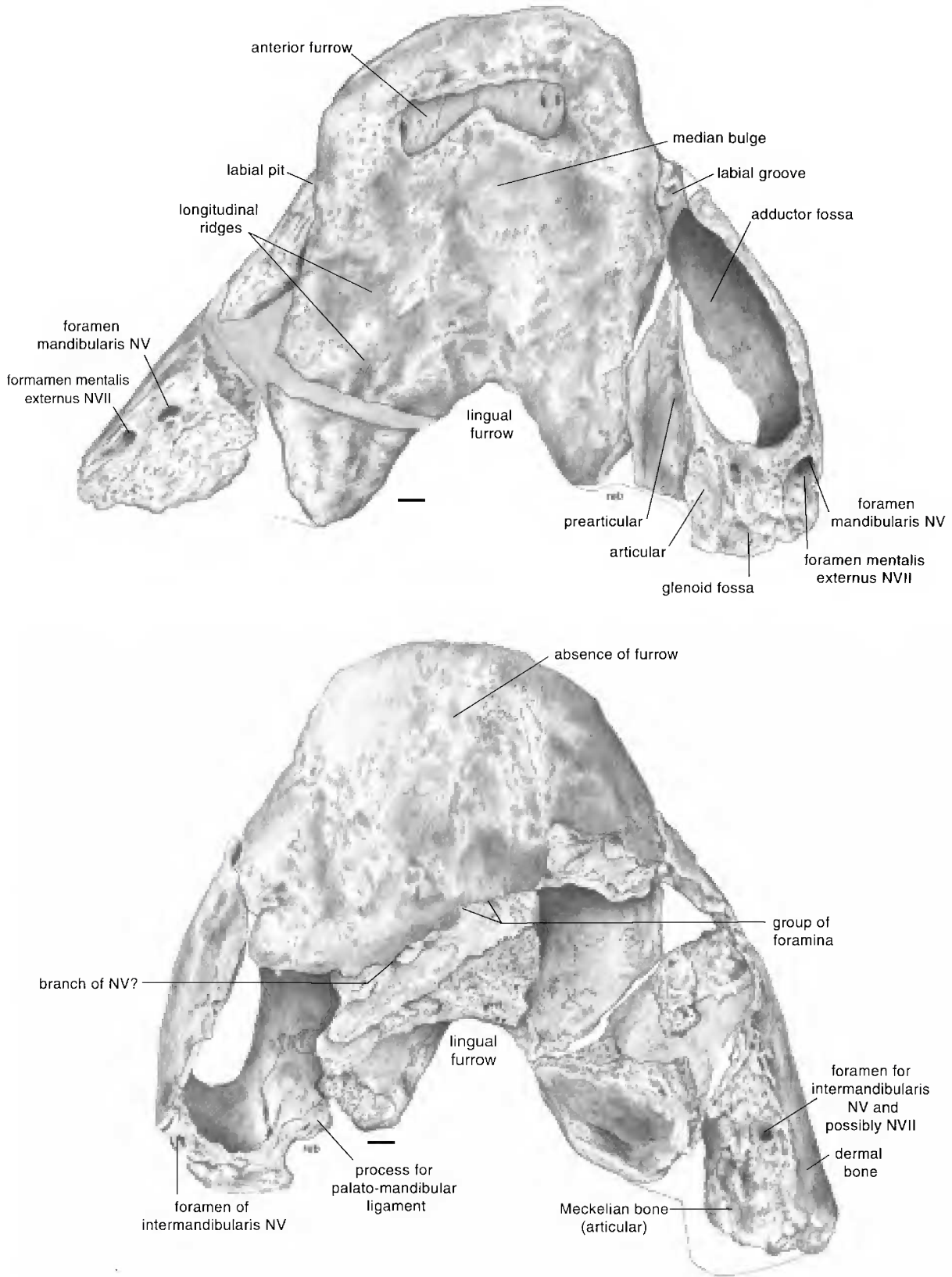


Figure 4. Reconstruction of the mandible of *Dipnorhynchus cathlesae* in dorsal and ventral views. The isolated part in the left side of the specimen did not fit back perfectly, and are shown in two slightly different positions on A and B. Scales = 1 cm.

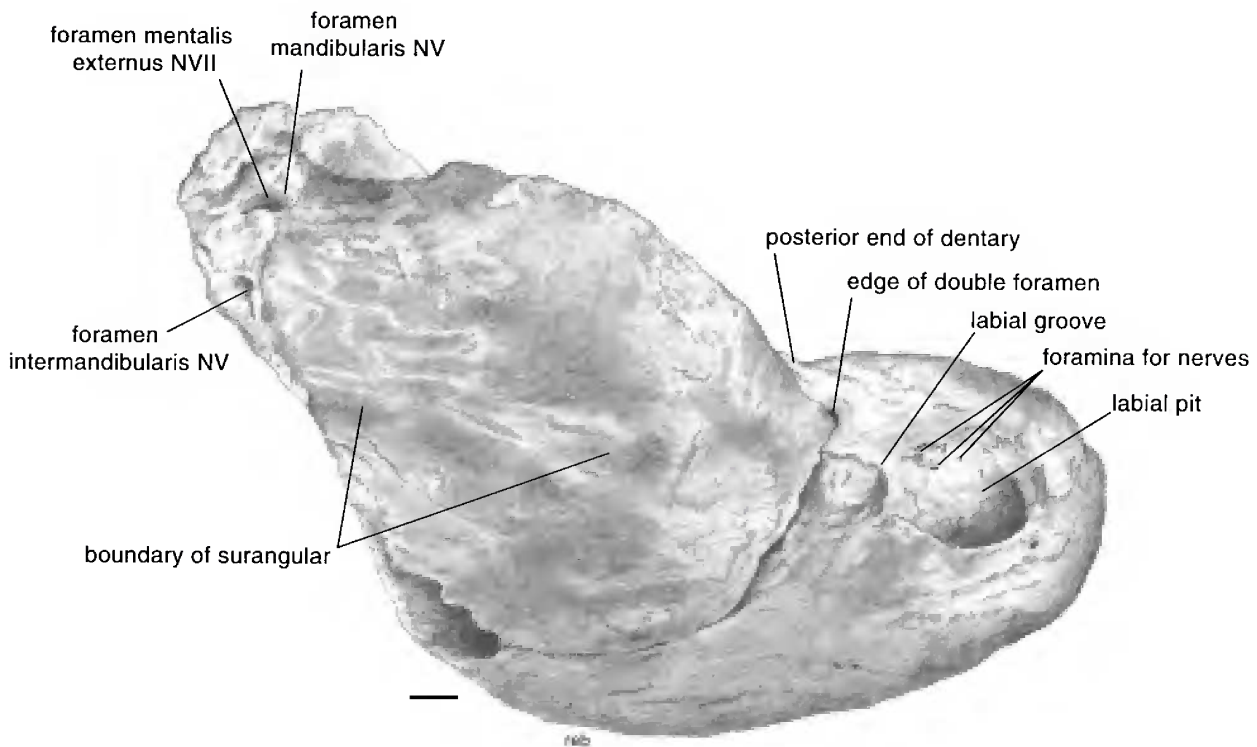


Figure 5. Right lateral view of the mandible of *Dipnorhynchus cathlesae*. The margin of the surangular is not clear and we have marked its ventral edge as “surangular” in its most probable position. Scales = 1 cm.

4. The **dental plate** (Figs. 3B, 4A, 7C) on the prearticular is up to 1.8 cm thick. It does not have any thick tubercles (or blisters; see White, 1966) such as occur in other dipnorhynchids. Surprisingly, this statement includes the large posterior tubercles (or blisters) as well as the anterior tubercles behind the anterior furrow. Is it possible that large tubercles were present originally, but have been removed by wear? Remaining on the surface are two or three low rounded longitudinal ridges, and a flattened median elevation behind the anterior furrow. In another work, we have shown that the eminences on the tooth plates in dipnorhynchids were formed by the addition of new tissue to the surfaces by upgrowth of new tissue on top of the underlying bones (Campbell & Barwick, in press), and in the discussion below, we discuss this matter further. Such eminences were modified by wear, but they were renewed on their surfaces by deposition from bony tubes through the underlying bone. Were the prearticulars smooth because of wear or because they were always without eminences? We have examined 12 mandibles of other dipnorhynchids, and on every one of them there is clear evidence of tubercles (blisters), even if they have been worn. Hence *D. cathlesae* is unique among dipnorhynchids in the structure of this part of its dental plate. Moreover the specimen has a distinct groove in the surface where other species have an anterior tubercle. So far as we are able to determine, this means that the dental surface was approximately flat, rather than tuberculate, throughout growth, and that the species crushed its food on a simple irregular grinding surface.

The margins of the prearticular against the adductor chamber consist of a sharp ridge without any sign of a rounded biting surface. Posteriorly this sharp ridge, formed by the junction of the dentine with the underlying bone, falls steeply into the posterior surface of the prearticular plate. The posterolateral surface adjacent to this dentine edge, makes a concave face medial to the glenoid fossa, and contains a wide open bony furrow which seems to have been floored, at least in part, by the articular laterally and the prearticular ventrally. The anterior part of this furrow has a broad shallow pit in which two or three nutrient openings are found (Fig. 6F). The posterior end of the structure is broken through, and clearly shows the coarse articular bone extending ventrally beneath the prearticular. Other well-preserved dipnorhynchids do not have a furrow in this position. On the contrary, the area is smooth, and passes posteriorly into the ridge on which was attached the pterygoid-mandibular ligament. Only the base of the pterygoid-mandibular ligament remains after breakage in *D. cathlesae*. The furrow described above must have been occupied by thick soft tissue forming the inner face of the glenoid fossa.

Although the glenoid fossa is not well preserved, it is known to be a posterodorsally directed opening, and is confined medially by a low bony ridge (Figs. 3B, 6F). Although the lateral and rotational movement of the mandible must have been controlled by the adductor muscles and a pterygoid-mandibular ligament, we also consider that the thick band of tissue in the position indicated would have served as a stabilising feature, confining the medial boundary of the glenoid fossa. The pressure on the

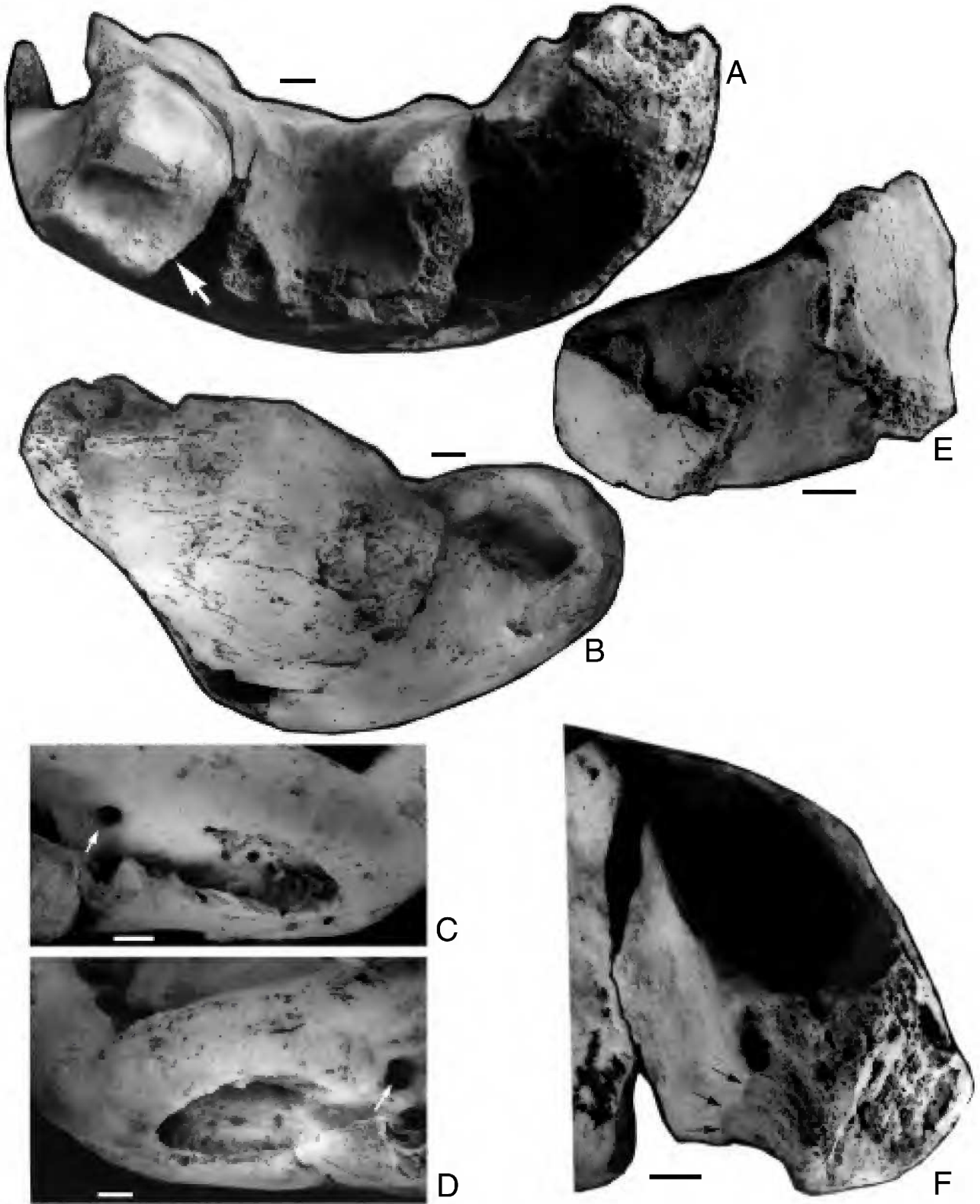


Figure 6. *Dipnorhynchus cathlesae*: A, posterior view; B, lateral view; C, D, dorsolateral views into the right and left labial pits. Note the foramina in the floors of the pits and the large foramina at their posterior ends, indicated by a white arrow in C and D. E, part of the mandible from the left side which was found down slope from the main specimen. Its position is shown by the large white arrow in Fig. 6A. Left side is external dermal bone; right side is the posterior face of the prearticular to the top left of the white arrow in Fig. 6A. Medial surface is where external bone was stripped off during preservation. F, right posterior end of the mandible showing the broken glenoid fossa, the sharp edge on the tooth-plate against the adductor fossa, and the sharp edged groove between the tooth-plate and the glenoid, marked by black arrows. Scales = 1 cm.

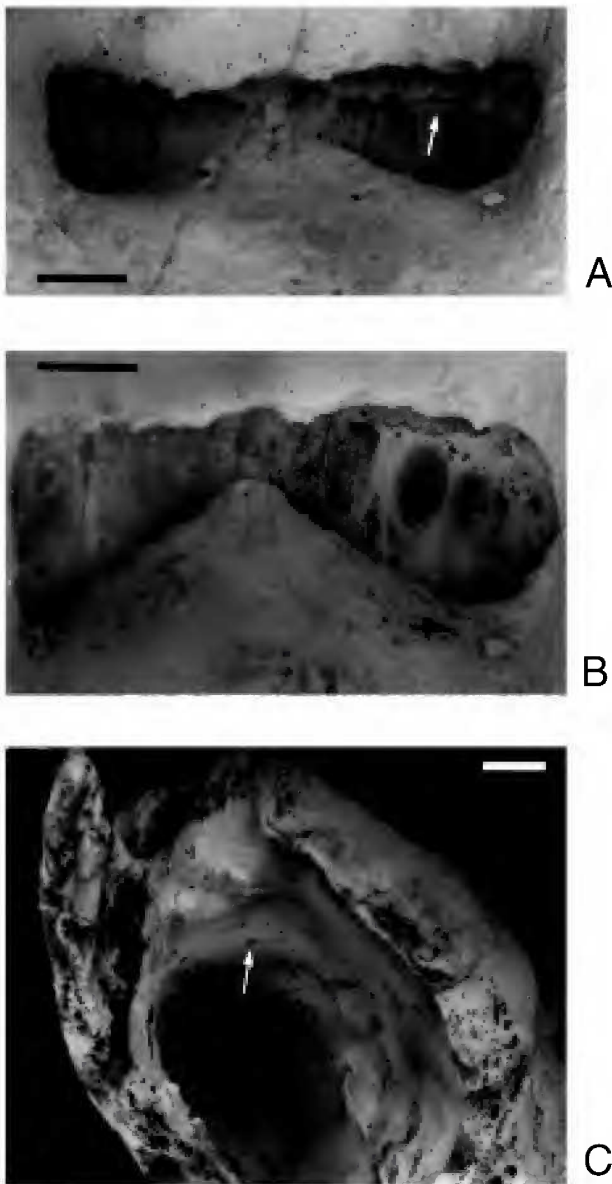


Figure 7. Two views into the anterior furrow of *Dipnorhynchus cathlesae*. A, with the specimen horizontal and B, with it tilted forwards. Note the abundance of pits on the right side and their scarcity on the left. The line of junction between the dentary and the endocranial bone shown by a white arrow. C, view down the adductor chamber on the left side of the specimen. The thickened prearticular is on the right. Note the ridges on the right wall, and the foramen (white arrow) with a short groove leading to the foramen at the posterior end of the labial pit. Many other nutrient foramina are also shown. Scales = 1 cm.

glenoid during a bite must have been very strong, and if large prey were being ground up on the dental plates, one would expect rotational forces to be periodically increased. Under these conditions, it is not surprising that extra support of the glenoid was developed.

The anterior end of the tooth plate is triangular in outline, but it does not rise up towards the dentary. On the contrary it declines perceptibly towards the anterior furrow, leaving

behind it a gentle, rather flattened eminence. Against the anterior furrow, the tooth plate strongly overhangs the underlying endoskeletal bone.

We note that in *D. kurikae* the margins of the dental plate show signs of active growth and modification. In particular this applies to a small patch of the plate medial to the glenoid fossa, and along the posterior edge of the plate within and lateral to the lingual furrow. At these localities the continuous layer of dentine has a sharp margin, and patches of rounded or slightly elongate denticles occupy the surface. These indicate that the plate was growing at these points when death occurred. In *D. cathlesae* no denticles are present posterolaterally, but some are present within the lingual furrow along the edge of the plate.

5. **A section of the dental plate** (Figs. 11–14) cut near the posteromedial part of the plate, shows the arrangement of the tooth plate, the prearticular and the Meckelian bone. This section passes from the about the mid-length of the adductor opening to the lingual cavity, but it is sufficiently central to be considered as typical of the tooth plate. The specimen was studied in an optical section and from a surface cut parallel to this one and studied by SEM. The optical section clearly shows the presence of irregular canals that probably represent the sites of activity of microorganisms, possibly fungal hyphae. Such features are known in other sections made from *Dipnorhynchus* specimens found at Wee Jasper and Taemas.

Deep weathering of the plate occurs along the medial side of the section, and along the dental surface, but fortunately some of this weathering is outside the main area of tooth-plate development. Peculiarities of the tooth plate have been recognised by workers on *Dipnorhynchus* since White (1966: 7) made the following comments: “the lower jaws of *Dipnorhynchus sussmilchi* ... do not shew tooth-plates with separate denticles but a crushing surface of raised blisters, large in extent but almost featureless, formed by a thickened layer of dentine continuous with the supporting bone.” Clearly he thought that the material of the tooth-plate was dentine. The section accompanying that description (White, 1966: fig. 1) shows a cross section of the large rounded “blister” forming the posterior part of a tooth plate. The material referred to as “dentine” consists of long narrow tubes which extend to the surface of the tooth-plate, though some surface decomposition of the tissue took place before collection. No evidence of a basal pulp cavity is present. We have specimens of *D. kurikae* which show similar arrangements.

Naturally this kind of tooth-plate cannot grow in the same way as the plates of later dipnoans, because there is no addition of marginal teeth to permit lateral growth and no median suture to permit internal growth. Furthermore the blister-like tubercles on the plates of *D. sussmilchi* and *D. kurikae* increased their height and their palatal shape without being at the plate margin. Some of these blisters have a “botryoidal” appearance in oral view (Campbell & Barwick, 1985: figs. 8d, 9a) indicating that their buccal surfaces grew from several sites. In the absence of a pulp cavity, we must begin to be concerned that the material called “dentine” is not dentine of the kind as occurs in later dipnoans.

In *D. cathlesae*, the thin tubes of tissue forming the

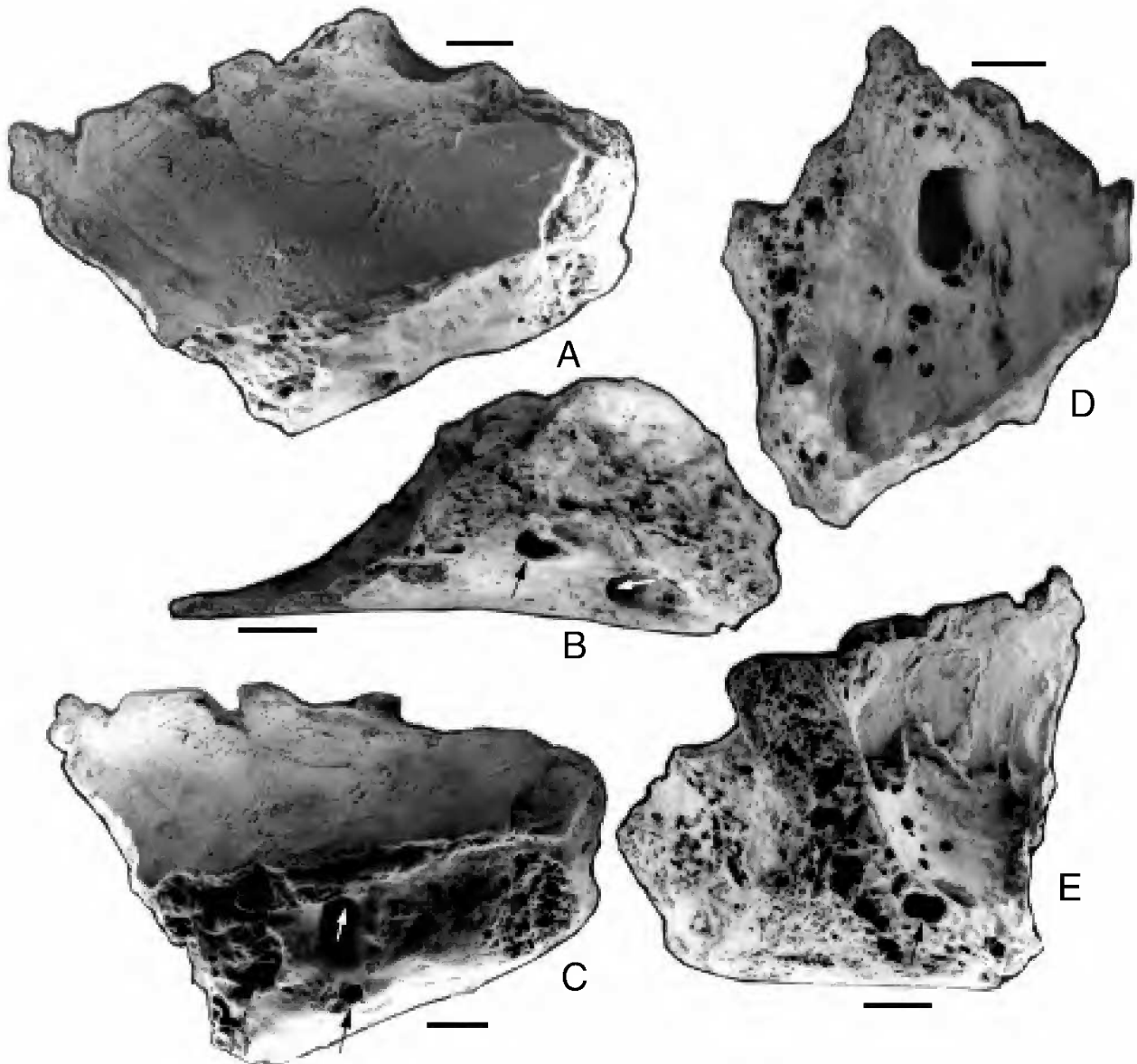


Figure 8. Views of the broken off fragment from the left corner of the specimen of *Dipnorhynchus cathlesae*. A, lateral view showing Westoll lines; B, dorsal view with the foramina for the ramus mandibularis V shown with a black arrow, and for the ramus mentalis externus VII shown with a white arrow; C, ventrolateral view showing the thick Meckelian bone with the large foramen for the ramus intermandibularis V shown with a white arrow, and a much smaller foramen for the ramus mentalis internus VII shown with a black arrow. The opposite end of the same canal is shown in E with a black arrow. D, E, two views of the internal surface showing the large foramen through which the nerves V and VII pass into the adductor chamber. Black arrow indicates the position of the ramus mentalis internus VII on the inner surface. Scales = 1 cm.

blisters have an irregular arrangement, but most of them are long and thin. A vertical section shows everything from longitudinal to transverse sections of the cavities. These cavities are filled with sediment, and some are branched. The walls are light coloured, but around the central canals is a darker layer. In several parts of the section, the hard tissue has strong concentric lines which indicates that recrystallisation has not taken place. These hard tissues should show dentine tubules, if the tubes are made of dentine, but in *D. cathlesae* no evidence of dentine tubules can be found, although it is clear that recrystallisation was **not** a factor in destroying fine structures. The absence of dentine tubules and the fact that reorganisation of the surface

of the dental-plates took place merely by upward growth from preexisting bone, indicates that the tooth-plate grew by growth from the underlying bone. We deal with this problem in a publication on *D. kurikae* (Campbell & Barwick, in press).

The inner face of the prearticular is covered with bone of a different character. It is distinguished in thin section by layers of bone lying slightly oblique to the depositional surface, the layers being joined by short vertical struts. As shown on Figs. 11A,C, a thin layer without bone lies between this material and the prearticular. However, it is not continuous along the whole length of the section and it passes into lamellated bone at each end. We consider that

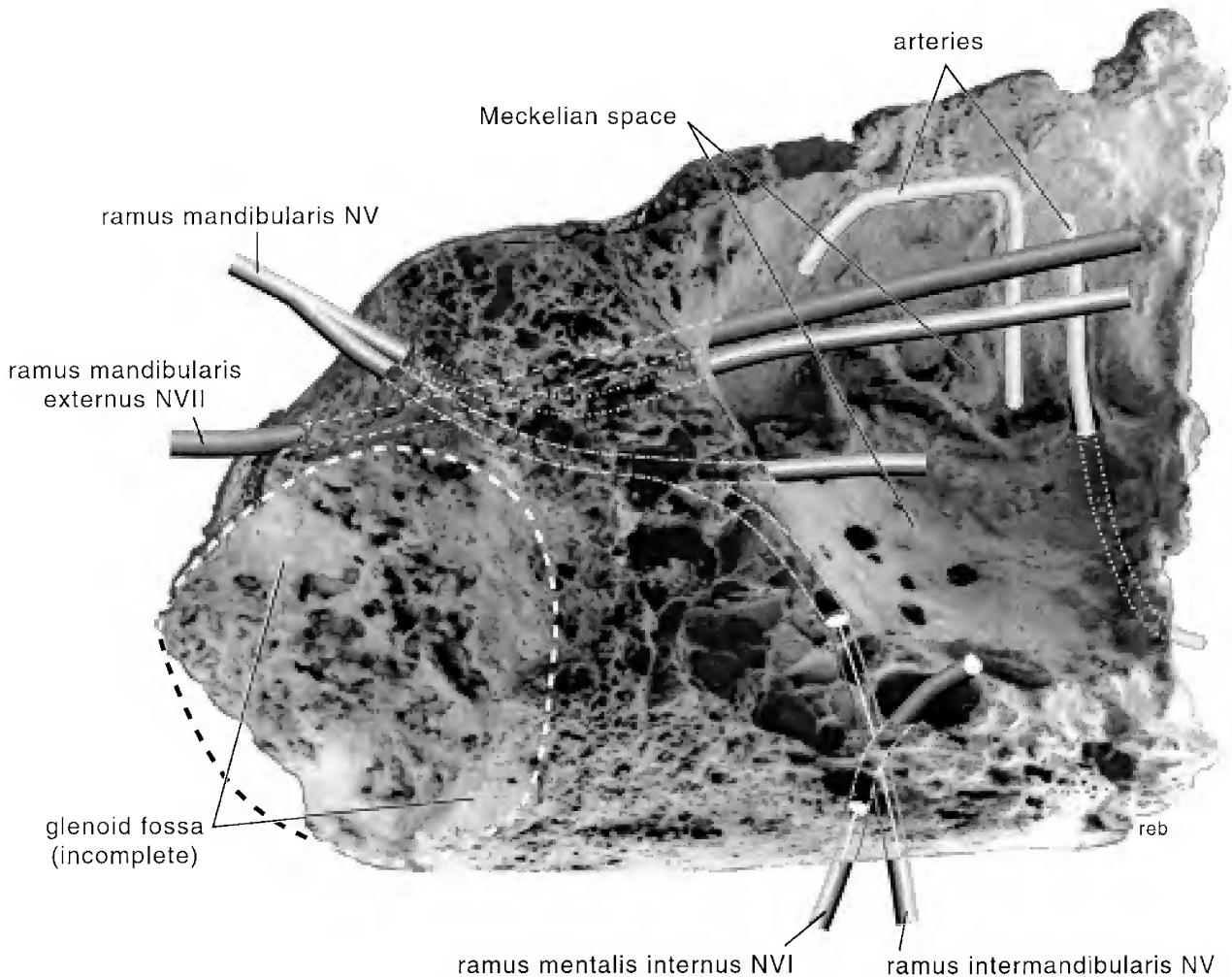


Figure 9. Reconstruction of the structures illustrated in Figs. 8D,E. Tubes buried in bone are indicated by broken lines. The glenoid is incomplete and is shown by a heavy dashed line. Two branches are shown for the ramus mandibularis nerve V whose paths are shown on the specimen. The internal branching of NV is well shown on the specimen. The arteries on the inner face of the surangular are shown by shallow grooves, and their paths are indicated.

the gap represents the sites of cells resorbing the Meckelian bone prior to deposition of new prearticular bone. The spaces between the bone layers are elongate. Optical sections show strong lines of growth parallel with the length of the lamellae, and these contain spaces which are also parallel with the lamellae (Figs. 11C, 12D, 14A). These are probably osteocyte spaces, and with the lamellar structure give an appearance which is quite different from that of the bone spaces in the prearticular bone. Is this bone a precursor of the prearticular, or is it a lining of Meckelian bone which occurs around the adductor chamber in other dipnoans? We know of no instance where a precursor of a dermal bone was laid down in bone which is so different in bone so different from the dermal bone itself. Observation of the interior of the adductor chamber shows that the layer runs forwards and around onto the external bone in the normal way that Meckelian bone does. Hence this seems the most appropriate name for the bone.

Between the thin-layered Meckelian bone and the main bone of the prearticular, there is a linear series of bone layers more widely separated than those in the Meckelian bone

(Figs. 11A,C). These lines of bones are gradually disappear laterally towards the inner edge above the posterior face of the mandible. The separation of bony layers is greater than in the Meckelian layers, and the openings between the layers is more elongate and thicker. These inner layers give the appearance of older Meckelian bone layers which have been partly modified by later activity of bone deposition. We note also that these lamellae have a similar internal structure to the main Meckelian bone, and it is easily distinguished from the intergrown porous bone which invades it.

Meckelian bone was thickened along the surface bordering the adductor chamber as would be expected. The prearticular thickens by resorption of the inner surface of the Meckelian bone and replacement by vascular bone of the usual prearticular type. This is seen particularly well on Fig. 11C. The thickness and the laminated texture of the Meckelian bone are possibly to be explained by the magnitude of the adductor muscles which were attached to it.

This interpretation is supported by our observations on the specimens of *Chirodipterus australis* and *Holodipterus gogoensis* etched from the Gogo faunas. In those species

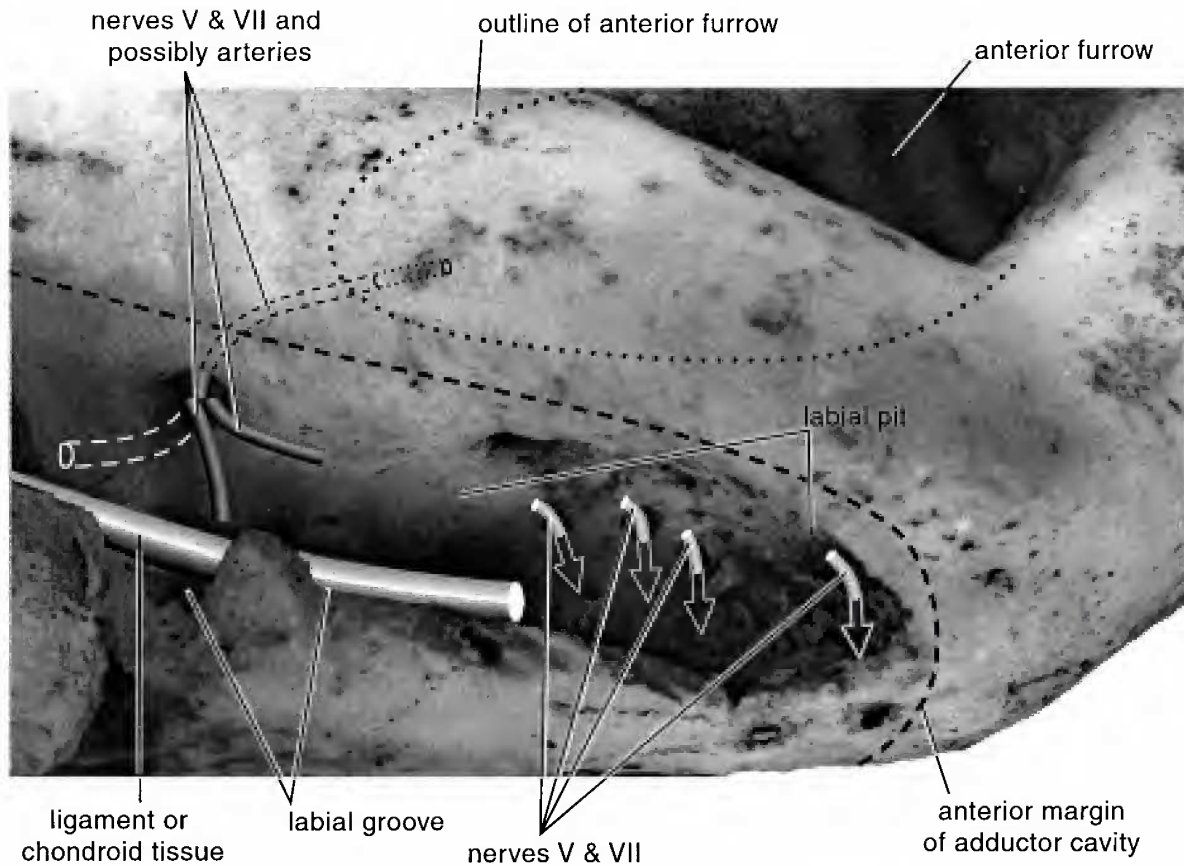


Figure 10. Reconstruction of the right labial pit showing the passage of the ligament or the chondroid tissue from the adductor chamber to the labial pit; some of the nerves V and VII running from the adductor cavity to the labial pit; and the nerves V and VII running through the large foramen at the posterior end of the labial pit and also into the anterior furrow. Parts of the canals buried in the bone are shown with a linear symbol or with a dotted margins.

much of the adductor space is lined by a thin layer of Meckelian bone which continues anteriorly from the articular bone. A gap is left between the prearticular and the inner lining of the Meckelian bone, and this must have been filled by the Meckelian cartilage. The prearticular was able to expand inwards by occupying this space and replacing the cartilage. The thin lining of the bone around the adductor chamber must have been resorbed and redeposited during growth. In *D. cathlesae*, no space was left to be occupied by the Meckelian cartilage. The Meckelian bone against the adductor chamber was much thicker than in the other two species, and continued to grow inwards as the prearticular expanded into the space previously occupied by Meckelian bone. This arrangement is interesting because it confirms the view that little growth took place on the buccal layers of the prearticular, and hence the absence of tubercles (blisters) on the grinding surfaces. Most of the thickening of the prearticulars took place by the rapid inward growth, occupying space originally occupied by Meckelian bone.

6. The **glenoid fossa** (Figs. 3B, 4A, 6F, 9) is not well exposed on either side of the specimen, but parts of both the articular bones remain. We have recently discovered that in *D. kurikae*, the preglenoid process has a strong

dorsally directed ligament attachment on its dorsal surface immediately inside the surangular. In *D. cathlesae* the surface of the articular in front of the glenoid fossa is flattened, and could have provided a surface for the attachment of a ligament. This surface is not extended forwards as a process plastered on the inner surface of the surangular on which ligaments could be attached, a feature found in other dipnorhynchids (Campbell & Barwick, 1985: figs. 8a, 9). Such a structure is exposed to weathering, and it could have been removed before collection of *D. cathlesae*. However, even if such a structure was not present, the articulation of the jaw would have been supported by the connective tissue forming the inner face of the glenoid region as shown in section 4 above. The matter will be further discussed in our paper on *D. kurikae*.

7. In dorsal view, the **adductor opening or fossa** (Figs. 3B, 4A, 6F) is pear shaped, being much wider posteriorly. Two cm from its posterior edge, it measures 4 cm across from crest to crest, and narrows gradually in front of that. This is a very different shape from the more parallel sided adductor opening in *D. kurikae*, in which the opening narrows down only within a short distance of the anterior end. In *D. cathlesae*, the lower medial wall of the adductor chamber formed by the inner face of the prearticular, is

very roughly ridged (Fig. 7C), almost to the anterior edge of the chamber. The coarse vertical ridges on the inner wall of the chamber extends much further forward than one would expect, reaching well up under the anterior furrow. Both sides of the specimen, but particularly the left, also have a few anteriorly directed ridges on the inner face of the outer wall of the chamber. On *D. kurikae* the ridging is not so powerful and does not extend so far up the inner face of the chamber. In *D. cathlesae* the adductor muscles were very strong and some of them were attached far forward of the anterior margin of the adductor opening, and on inner and outer sides of the adductor chamber.

In *D. kurikae*, the articular runs forwards along the edge of the prearticular on the upper edge of the adductor opening, making a distinct rounded ridge which shows so well in dorsal view. In *D. cathlesae*, the articular is present in this position, but it does not appear as a rounded ridge in dorsal view (Figs. 3B, 4A). The reason for this is that the prearticular rises high against the edge of the adductor chamber, and the articular is smoothed out against it rather than forming a rounded ridge. This feature is obviously related to the way in which the tooth plate comes to a crest along its lateral margin.

8. The **lingual furrow** (Figs. 4A,B) is slight, has an almost vertical lower face ventrally on the prearticulars, but turns over into a shallow groove dorsally. The lower vertical part is very high as compared with that of *D. kurikae*. The prearticulars forming the lateral parts of the front wall of the lingual cavity are thick, and they are deeply concave, overhung by a projection on the tooth plates.

The anterior space for the tongue is short and narrow, though the posterior part must have been wide. In the posterior face of the prearticular bone is a broad deep cavity into which the lateral parts of the tongue pad would have fitted. Judging from the position in extant dipnoans, the anterior part of the tongue would have been short, and would not have extended forwards into the space occupied ventrally by the rounded eminence in the median floor. The whole contour of this region indicates that the hyoid system would have been very posterior in position and would have had little opportunity to move dorsally and ventrally to control the buccal space. This emphasizes emphatically that the hyoid arch would not have been able to compress an air space in the back of the buccal cavity as would have been required for air breathing along the same lines as in extant dipnoans.

At their ventral edge on the posterior face of the mandible, where the prearticulars join the dermal bones, the prearticulars have a distinctive inturning towards the dermal bone. This leaves a flange around the specimen which is larger than any other species of the genus.

9. The **nerve canals** (Figs. 3B, 4A,B, 8, 9) lateral to the glenoid fossa are quite different on the two sides of the specimen. On the left, two large foramina lie between the articular and the surangular. The more posterior one is more laterally placed and passes posterodorsally into a deep groove which runs off the articular. It presumably contained a branch of the nerve ramus mentalis externus VII (*f me VII* of Thomson & Campbell, 1971). Note that Miles (1977:

fig. 102) has two branches of this nerve in *Chirodipterus australis*, but he was unsure about the significance of this because the two did not appear in all specimens. Internally this large foramen in *D. cathlesae* opened after a short course into a large chamber. Within this chamber the courses of the furrows are not clear, but the VIIth nerve enters a groove which ran down the inner face of the surangular bone. The dorsal one is small and lies at the top of the foramen and cannot be traced anteriorly. The lateral one lies against the surangular and continues along the inner face of that bone.

The more anterior foramen on the left side of the dorsal surface of the bone is of about the same size as the posterior one, but it passes through the articular in a more dorsomedial orientation than the ramus mentalis externus (*f me VII* of Thomson & Campbell, 1971), into the same large internal chamber. On the external surface this groove seems to be entered by two foramina, the anterior one being dorsally and the lateral one being posterodorsally directed. Its position in the chamber and anterior to it is not clear on the specimen, but it sends a groove down the inner face of the chamber to run to the foramen intermandibularis V (see below) on the ventral surface of the mandible. The anterior opening of the chamber shows a rounded edge indicating that a branch of nerve V passed into the adductor chamber away from its walls, and hence into the adductor muscles. Up towards the dorsal foramen, another branch joins the groove that carries the ramus VII forwards along the surangular. We consider that it carried the mandibularis V along with the mandibularis VII to the anterior end of the mandible.

Opening ventrally out of the mandible is a large rounded foramen in the articular, rather than at the junction between the dermal bone and the articular. It would have transmitted the intermandibularis nerve V (*f int V* of Thomson & Campbell, 1971). In addition to the V nerve, we expect from the above description that it also contained branches of the VII nerve. As would have been expected, the grooves leave this foramen in anterior, ventral and posterior directions innervating the elongate intermandibularis muscle.

Ventral to this foramen for the ramus intermandibularis V nerve (*f int V* of Thomson & Campbell, 1971) is a much smaller foramen which connects through the articular below the floor of the adductor chamber in a much larger foramen on the broken internal surface. The right side of the specimen apparently had a similar structure, but it has been broken through during preservation. A similar foramen has been recorded by Miles (1977) in *Chirodipterus* which he labelled *crc*, and he indicated only that it was the "posterior cross canal". He did not indicate the function of this structure. Because of its position and the presence of small openings in its wall making connections with the surrounding bone, we consider that this system contained a nerve. The canal is in an appropriate position for the ramus mentalis internus VII nerve, according to the reconstructions of *Neoceratodus* by Fox (1965).

Miles (1977: 204) commented that he considered the mandibularis V nerve to have passed through the adductor fossa, and that "all the openings in this region, in both *Dipnorhynchus* and *Chirodipterus* transmitted branches of the *R. mentalis externus VII*". Our specimen shows that the nerve V would not have passed in this way; indeed some of our specimens of *C. australis* indicate the same point. It

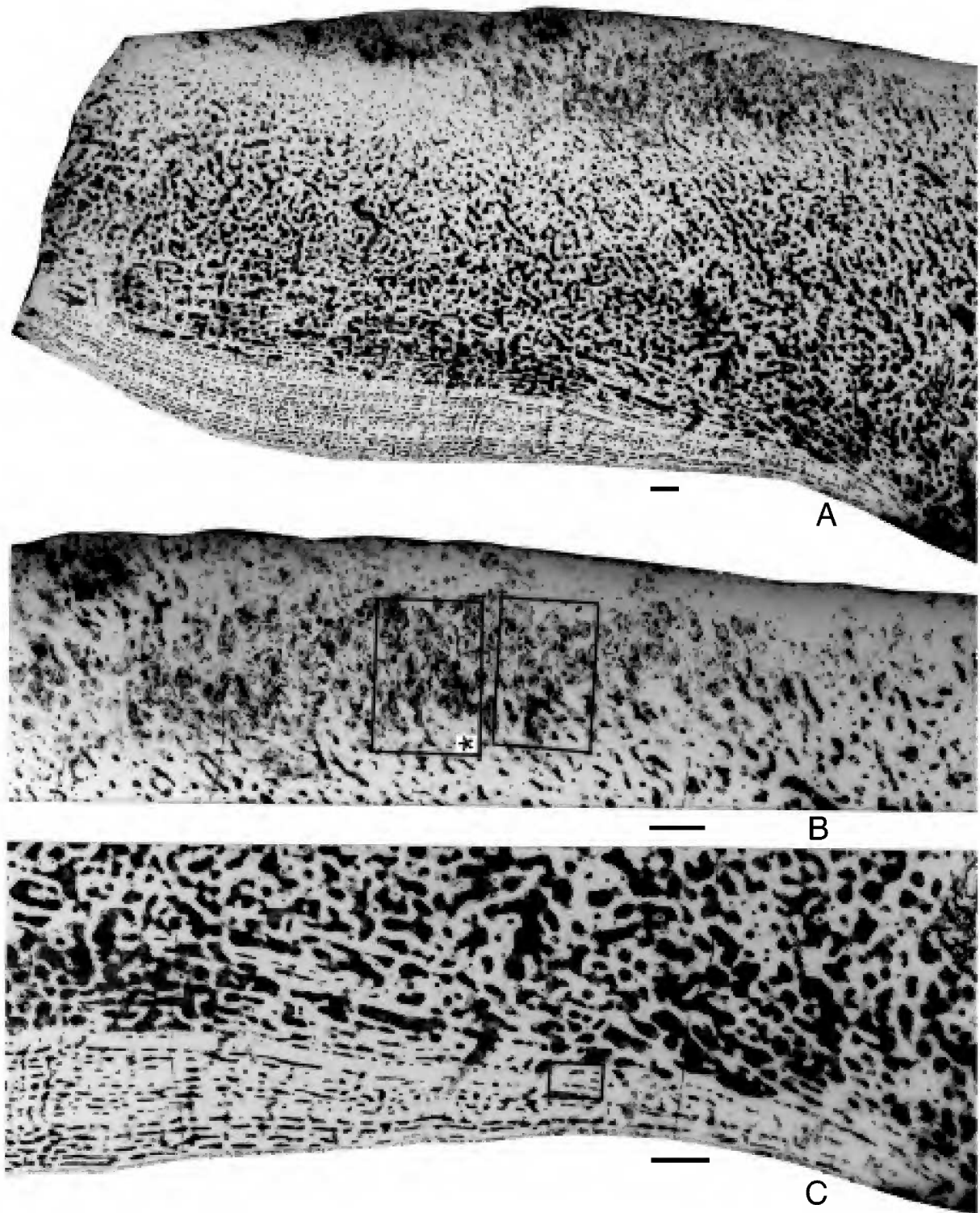


Figure 11. Sections of the prearticular of *Dipnorhynchus cathlesae*. A, transverse section as shown by the black arrow on Fig. 3B. The left side is towards the adductor fossa, and the right onto the posterior wall of the mandible. A thin layer of sediment is left attached to the base of the section. A, shows the Meckelian bone at the base overlain by thin layers of Meckelian bone being transformed into prearticular bone. At the top is a change in texture where the prearticular is replaced by so-called “dentine”. The boundary between the two tissues is marked by discontinuities. The topmost part of the section is so weathered that no detail can be seen in it. B, enlargement of the top of A showing the contact between the main bone of the prearticular and the so-called “dentine”. The uppermost surface is weathered. C, enlarged part of the Meckelian bone and contact with the prearticular. Note how the layers in the laminae change abruptly to become less continuous in the prearticular. Scales = 1 mm.

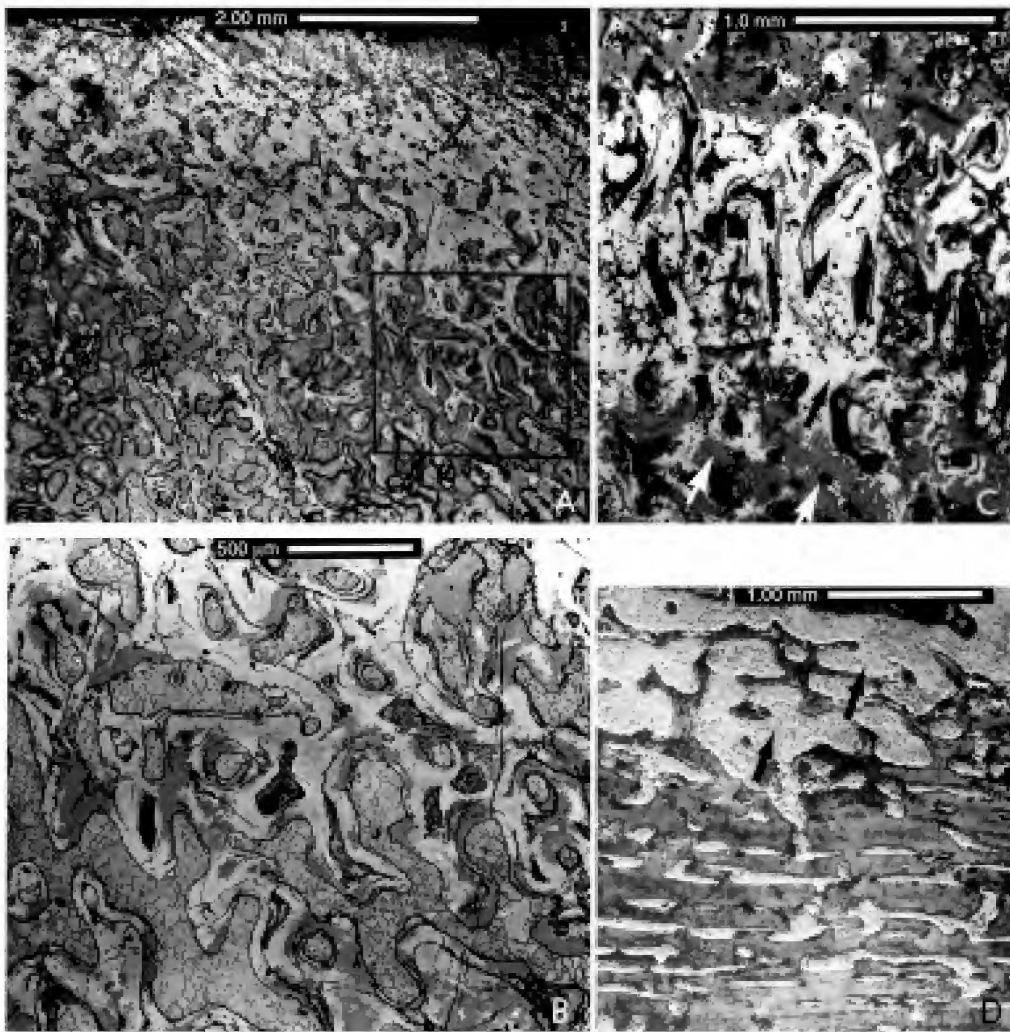


Figure 12. A–C, back scattered SEM figures taken from a slice cut parallel with the section in Fig. 11. A, shows the transition between the dark coloured bone at the base and the lighter coloured so-called “dentine” at the top. B, enlargement of the area shown on A. Note the absence of any continuous gap between the two types of tissue. The crazed pattern is calcite infilling the specimen. C, specimen of the tissue near the top of the section showing the elongate spaces in the so-called “dentine” (black arrow), and the bone at the base (white arrows). D, section through the Meckelian bone showing lamination and the abundance of elongate osteocyte spaces. Note the transition from the closely layered Meckelian bone at the base into the overlying bone. Black arrows indicate calcite infillings of the matrix.

will be obvious that we consider the complication suggested by Miles to be unnecessary, and that Thomson & Campbell (1971) were correct in having both nerves V and VII oriented as they suggested.

On the right posterodorsal side of *D. cathlesae*, there is a single opening which is larger than either of the nerve openings on the left side of the specimen. The inner wall of this opening has a ridge which separated the two nerves entering the foramen. The posterior opening is by far the smaller one and the more dorsal opening is almost vertical. We consider that these are for the ramus mentalis externus VII and the ramus mandibularis V respectively. The internal cavity within the articular is smaller than the one on the other side, and its anterior opening is also smaller.

10. The **infradentary bones** (Figs. 3A, 5, 6B) are moderately well exposed, especially on the right side of the

specimen. They were originally covered with cosmine, but wear has removed some of that tissue. On the right side the posterior part of the surangular is exposed. It has an acute posterior end which rises high on the side of the mandible and lies immediately beneath the foramen for the ramus mentalis externus VII. This is unusually high in comparison with *D. kurikae* and *D. sussmilchi*, in which a granulated surface occupies the upper part of the bone.

Westoll lines are obvious on the surangular on the left side (Figs. 8A,C). They close posteriorly where they turn upwards slightly to produce a banana shape. The ventral edge of the surangular is exposed incompletely on the right side of the specimen, and gives the impression that the bone runs forward to the ventral edge of the labial pit, though its anterior edge cannot be seen. This is appropriate for a dipnorhynchid, in which the surangular is always long. On the right side the lateral line canal is visible lying about half way down the bone.

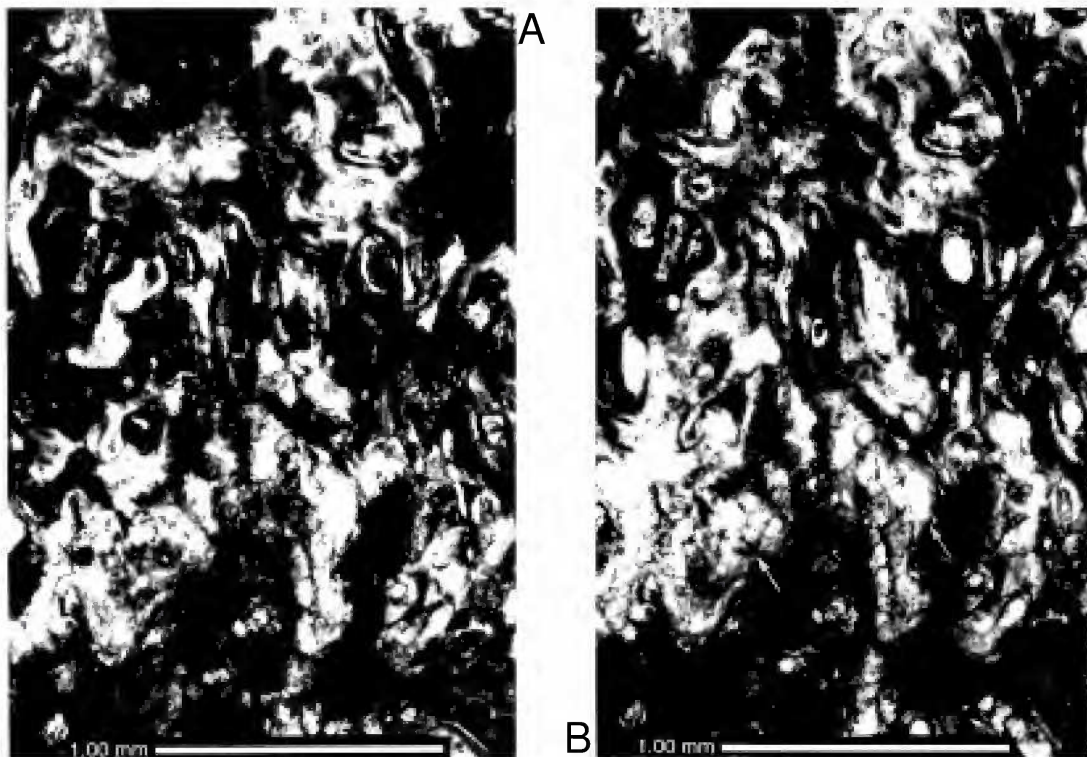


Figure 13. Two views of the one position of the optical section outlined in Fig. 11B marked with an asterisk. A, crossed polarised light and B, single polarised light. At the base the tissue is prearticular bone, and at the top it is the so-called “dentine”. The large areas marked with the white arrows are infillings of the open spaces between the bone and the so-called “dentine”.

11. Because the **posterior edges of the infradentaries** (Fig. 6A) are badly worn, it is not possible to give precise positions for all the foramina which usually occur along the line between the infradentaries on the one hand, and the prearticulars and the Meckelian bone on the other. In *D. kurikae*, the largest foramen along this line is figured by Campbell & Barwick (1985: fig. 8B), but it was unlabelled. Several other topotypes of *D. kurikae* have since become available, and all show this feature. *Dipnorhynchus sussmilchi* has a smaller foramen in this position, and one or two other foramina medial to it. The specimen of *D. cathlesae* is poorly preserved in this region on both sides of the specimen, but on the left side the broken surface shows a large foramen passing between the Meckelian bone and the infradentaries. It is a section across a canal which continues forward and enters the adductor chamber in a forwards position. This is in the same position as the foramen in *D. kurikae*, and the foramen for the efferent branchial artery in *D. sussmilchi* (Thomson & Campbell, 1971: fig. 22).

Specimens of *D. sussmilchi* show strong canals on the face of the prearticular in the adductor chamber (Thomson & Campbell, 1971: figs. 47–49). These develop from a foramen which lies between the postsplenic and the prearticular. A similar groove is found in *D. cathlesae* running up the surface through the bone forming the coarse ridges used for muscle attachment, then across the under surface of the dental plate and then into a fossa in the plate at the level of the anterior end of the adductor fossa. It enters a deep tube in the plate, and can be traced through

the plate in an anterior direction, emerging in the posterior corner of the anterior pit. Further back along this main canal where a sharp turn forwards occurs, a weaker canal runs forward along the line indicated by the symbol *sa1* by Thomson & Campbell (1971: fig. 22). The more posterior branch of the canal running to *f₁ sa 1* in *D. sussmilchi* is not well represented on our specimen, mainly because the specimen is poorly preserved in that region.

We point out that the canals as in *D. sussmilchi* have now been found in new specimens of *D. kurikae* and in *D. cathlesae*. No matter how we interpret these structures in functional terms, it is clear that they are features found in all dipnorhynchids.

Comparisons

In the above description we have concentrated on comparisons with *D. kurikae*, which is the species stratigraphically closest to *D. cathlesae*, and also occurs in the Wee Jasper sequence. The only other species in which the mandible is known is *D. sussmilchi*, the type species. This was described by Thomson & Campbell (1971). Since that time we have discovered three imperfect specimens of *D. sussmilchi* in the *Spinella yassensis* Limestone, some of which allow us to add to the previous description.

In *D. sussmilchi* the lingual furrow is deeper and proportionately narrower than that of *D. kurikae*. It continues forward as a distinct furrow to the anterior furrow which lies just medial to and slightly behind the end of the

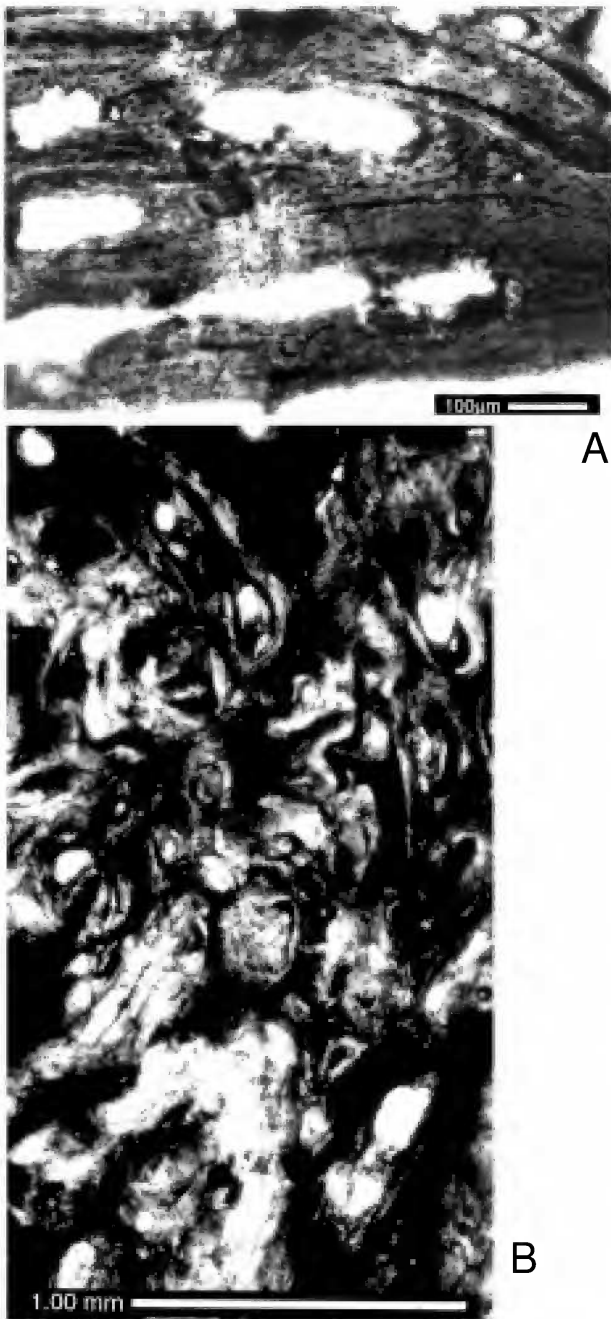


Figure 14. A, enlarged part of the Meckelian bone (outlined on Fig. 11C). It shows the lamination and the abundant osteocyte spaces. B, section under crossed polars. Its position is the right rectangle shown on Fig. 11B. It crosses the boundary between the prearticular bone at the base and the so-called “dentine” at the top. The two images are reversed in comparison with Fig. 11.

anterior furrow. Posterior to this is a deep groove, the inner edge of which is well defined by a ridge that extends back to the large rounded posterior protuberance forming the main grinding face of the tooth plate. In all these features, *D. sussmilchi* is unlike *D. kurikae*, and even less like *D. cathlesae*. Like *D. kurikae*, *D. sussmilchi* has a similar groove running between the lateral margin of the tooth plate

and the posterior protuberance. We have also noticed that the articular has a projection in front of the glenoid fossa to which was attached a muscle as in *D. kurikae*. This is not present to anything like the same extent on *D. cathlesae*. Finally, the lip pit on *D. sussmilchi* has a well-rounded anterior edge and does not extend into a furrow as in the other species.

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